Affective Judgments of Faces Modulate Early Activity (~160 ms) within the Fusiform Gyri

Diego A. Pizzagalli,*,†,‡ Dietrich Lehmann,†,§ Andrew M. Hendrick,* Marianne Regard,†
Roberto D. Pascual-Marqui,§ and Richard J. Davidson*,‡,¶

*Department of Psychology, ¶Department of Psychiatry, and ‡W. M. Keck Laboratory for Functional Brain Imaging and Behavior,
University of Wisconsin, Madison, Wisconsin 53705; †Department of Neurology, University Hospital, Zurich, Switzerland;
and §The KEY Institute for Brain–Mind Research, University Hospital of Psychiatry, Zurich, Switzerland

Functional neuroimaging studies have implicated the fusiform gyri (FG) in structural encoding of faces, while event-related potential (ERP) and magnetoencephalography studies have shown that such encoding occurs approximately 170 ms poststimulus. Behavioral and functional neuroimaging studies suggest that processes involved in face recognition may be strongly modulated by socially relevant information conveyed by faces. To test the hypothesis that affective information indeed modulates early stages of face processing, ERPs were recorded to individually assessed liked, neutral, and disliked faces and checkerboard-reversal stimuli. At the N170 latency, the cortical three-dimensional distribution of current density was computed in stereotactic space using a tomographic source localization technique. Mean activity was extracted from the FG, defined by structure-probability maps, and a meta-cluster delineated by the coordinates of the voxel with the strongest face-sensitive response from five published functional magnetic resonance imaging studies. In the FG, ~160 ms poststimulus, liked faces elicited stronger activation than disliked and neutral faces and checkerboard-reversal stimuli. Further, confirming recent results, affect-modulated brain electrical activity started very early in the human brain (~112 ms). These findings suggest that affective features conveyed by faces modulate structural face encoding. Behavioral results from an independent study revealed that the stimuli were not biased toward particular facial expressions and confirmed that liked faces were rated as more attractive. Increased FG activation for liked faces may thus be interpreted as reflecting enhanced attention due to their saliency. © 2002 Elsevier Science (USA)

INTRODUCTION

Faces convey a wealth of information, including gender, age, expression, eye gaze, race, and personal identity, all of which are critical for adaptive social interaction. Since faces are endowed with remarkable social meaning, one may assume that specialized brain processes have evolved for rapid and reliable processing of affective and socially salient information. In humans, functional neuroimaging studies have identified a region in the ventral occipitotemporal cortex around the lateral fusiform gyrus (FG) that responds preferentially to faces compared to other classes of visual objects (Puce *et al.,* 1996; Kanwisher *et al.,* 1997; McCarthy *et al.,* 1997; Aguirre *et al.,* 1999; Haxby *et al.,* 1999; see Haxby *et al.,* 2000, for review). Although the functional role of the FG remains controversial (Kanwisher, 2000; Tarr and Gauthier, 2000), this region may be involved in relatively early perceptual processing of faces, such as structural encoding[1] of the information required for face recognition (Tong *et al.,* 2000; George *et al.,* 1999).

Recordings of brain electromagnetic activity have complemented these results by providing crucial information about the temporal unfolding of brain mechanisms involved in face processing. Event-related potential (ERP) (Bentin *et al.,* 1996; Eimer, 2000; Mouchetant-Rostaing *et al.,* 2000; Rossion *et al.,* 2000) and magnetoencephalography (MEG) (Sams *et al.,* 1997; Streit *et al.,* 1999; Watanabe *et al.,* 1999; Halgren *et al.,* 2000; Liu *et al.,* 2000) studies have identified a posterior-lateral negative peak at a latency of approximately 170 ms (the so-called "N170") that was elicited by faces but not by other control stimuli. As the N170 was found to be unaffected by face familiarity, it seems to be associated with precategorial structural encoding of faces rather than with later processes involved in face recognition or identification (Bentin and Deouell, 2000; Bentin *et al.,* 1996; Eimer, 2000). Similar conclusions were drawn from intracranial ERP studies in

---

[1] According to an influential model of face recognition (Bruce and Young, 1986), structural encoding refers to the extraction of physiognomic characteristics needed for forming an internal representation of faces.

medicated epileptic patients, in which a face-sensitive, surface-negative potential was recorded from the ventral occipitotemporal cortex (particularly, lateral FG) peaking at approximately 200 ms poststimulus (Allison *et al.,* 1999; McCarthy *et al.,* 1999; Puce *et al.,* 1999). Overall, these studies suggest that the lateral FG may be involved in structural encoding of faces and that the N170 may be a neurophysiological manifestation of these processes.

Several lines of evidence suggest that processes involved in face recognition may be strongly modulated by affective information conveyed by faces. First, behavioral studies in normal subjects (e.g., Bradley *et al.,* 1997) and in brain-damaged patients with spatial neglect (Vuilleumier and Schwartz, 2001) suggest that emotional stimuli capture attention more readily than neutral stimuli. Second, functional neuroimaging studies have found that face-sensitive FG activity can be modulated by socially relevant information and by attentional manipulations. Indeed, increased FG activation has been reported for emotional vs neutral faces (Breiter *et al.,* 1996; Dolan *et al.,* 1996; Morris *et al.,* 1998; Critchley *et al.,* 2000; Hariri *et al.,* 2000), directed vs averted eye gaze (George *et al.,* 2001), same race vs other race of the face (Golby *et al.,* 2001), intentional encoding vs passive viewing of the faces (Kuskowski and Pardo, 1999), and covert attention toward vs away from faces (Wojeiulik *et al.,* 1998). Third, and consistent with the view that processing of affective and socially salient information may be very rapid, recent ERP and MEG studies have found that affective (Pizzagalli *et al.,* 1999, 2000: 80–160 ms; Streit *et al.,* 1999: 160 ms; Halgren *et al.,* 2000: 110 ms; Halit *et al.,* 2000: 170 ms) and gender (Mouchetant-Rostaing *et al.,* 2000: 145–185 ms) discrimination start very early in the human brain. Whereas the functional neuroimaging results raise the possibility that structural face encoding and encoding of socially salient information may cooccur in space, time, or both, their coarse temporal resolution does not allow for excluding that these effects were caused by feedback projections from brain regions encoding affect or other salient information at later stages. Conversely, the ERP and MEG results suggest that such information may modulate structural encoding.

In the present study, we investigated the effect of liking on face processing. We reasoned that if affect is extracted very rapidly (<120 ms), as recent studies suggest (Halgren *et al.,* 2000; Pizzagalli *et al.,* 1999), then this information may modulate later processes implicated in structural facial encoding (~170 ms). Further, we investigated liking judgments, as one of the most remarkable characteristics of affect is how individuals react differently to the identical affective stimuli (Davidson and Irwin, 1999). Since prior research has shown that both negatively (Breiter *et al.,* 1996; Hariri *et al.,* 2000) and positively (Dolan *et al.,*

1996; Morris *et al.,* 1998) valenced stimuli modulated FG activity, no specific predictions were advanced as to whether individually assessed liked or disliked faces would elicit stronger FG activity. To test whether face-sensitive N170 activity within the FG can be affect-modulated, we used a new tomographic source localization technique based on realistic head geometry and probabilistic brain atlases, low-resolution electromagnetic tomography (LORETA; Pascual-Marqui *et al.,* 1994, 1999). The sensitivity of this tomographic source localization technique was additionally increased by restricting the source analysis to activated face-sensitive voxels of published functional magnetic resonance imaging (fMRI) studies.

MATERIALS AND METHODS

Subjects

Eighteen (7 female) healthy, right-handed (Oldfield, 1971) volunteers (age (years): mean (M) = 29.4, SD = 4.9) with no history of neurological or psychiatric disorders participated in the ERP study. The study was approved by the Local Ethics Committee (University of Zurich), and subjects gave informed, written consent. The analyses reported here are based upon the same subjects as were included in Pizzagalli *et al.* (2000).

Twenty-three undergraduate students from the University of Wisconsin-Madison (14 females; age (years): 23.3 ± 3.9) volunteered to participate in a behavioral study involving affective ratings of the facial stimuli used in the ERP study.

Electroencephalogram (EEG) Acquisition

EEGs were recorded from 27 electrodes according to the extended 10/20 system: Fpz (recording reference), Fp1/2, Fz, F3/4, F7/8, FC1/2, Cz, C3/4, T7/8, CP1/2, Pz, P3/4, P7/8, PO3/4, Oz, and O1/O2. Eye movements were recorded from the outer left canthus referenced to Fpz. Impedances were kept below 5 kohms. The data were amplified (0.3–70 Hz) and digitized (256 samples/s) with a 31-channel BioLogic Ceegraph System.

Procedure and Stimulus Material

Subjects were seated in a sound, light, and electrically shielded room equipped with an intercom system. A chin rest was used to keep the distance between the subject and the screen constant (100 cm). Before the main experimental recording, the subjects' ERPs were recorded during a control condition for visual input. The subjects passively observed emotionally neutral, visual checkerboard-reversal stimuli on a computer monitor (200 reversals; frequency: 2 Hz). Subsequently, subjects were instructed to passively observe faces serially presented on the monitor. Subjects were naïve to the face images, which consisted of 32 black

and white digitized photographic portraits of psychiatric patients ("Szondi portraits") particularly suited to evoke emotional decisions (Regard and Landis, 1986; see Pizzagalli *et al.,* 1999, for examples of the stimulus material). These stimuli do not possess marked facial expressions (see below) and thus are well-suited to the investigation of individual differences in affective judgments. The stimuli were size-, contrast-, and brightness-adjusted portrait photographs (8 × 11 cm). Stimuli, which extended 4.57° of visual angle horizontally and 6.28° vertically, were presented for 450 ms separated by 2000-ms intertrial intervals centered in a continually visible frame (18.8 × 12.5 cm) on a light gray background. Twenty randomized blocks of the 32 faces were presented with 1-min intervals between blocks.

Affective Ratings

Following ERP acquisition, subjects rated each stimulus for its affective appeal. They were instructed to judge how much they liked or disliked each face using a 10-cm visual analog scale anchored with the labels "liked face" and "disliked face." Each stimulus was presented on individual hard copy, with the analog scale to the right. A unique randomized order was used for each subject.

For the independent behavioral study performed at the University of Wisconsin-Madison, subjects were asked to rate each of the original 32 faces with respect to like/dislike, discrete facial expressions (fear, anger, surprise, disgust, sadness, happiness), and attractiveness. Each face was presented on individual hard copy, with the following eight analog scales to the left: "How much do you like/dislike this face?" (from 0, "*dislike very much*" to 10, "*like very much*"), "How fearful (angry/surprised/happy/disgusted/sad) does this person look?" (from 0, "*not at all*" to 6, "*very much*"), and "How attractive is this face?" (from 0, "*very unattractive*" to 10, "*very attractive*").

Data Reduction

After off-line automatic artifact rejection (epochs containing amplitudes exceeding 150 μV in the EEG channels or 70 μV in the electrooculogram channels were dropped), ERPs covering 1024 ms poststimulus were averaged for each subject using the idiosyncratically assessed 10 most-liked and 10 most-disliked faces (using all 20 blocks). [In a previous study (Pizzagalli *et al.,* 1999), we found that habituation effects did not reduce early affect-modulated ERP activity. Based on these results and to increase the signal-to-noise ratio in the current study, ERPs to faces presented in all 20 blocks were analyzed]. The number of artifact-free epochs used for computing the ERPs was closely matched for liked (158.8 ± 21.9) and disliked (159.0 ± 21.6) faces.

For each subject, three additional ERPs were computed: one for the checkerboard-reversal stimuli, one for faces rated as affectively neutral (i.e., between 4.5 and 5.5 on the analog scale), and one for liked or disliked faces associated with normally distributed ratings (across subjects) around the midpoint of the rating scale. These control ERPs were used to assess the specificity of putative results. The ERPs to checkerboard-reversals were used to test whether facial stimuli elicited stronger activity in face-sensitive cortical regions compared to a nonfacial control stimulus. The ERPs to neutral faces were used to test whether affectively laden facial stimuli elicited stronger activity in face-sensitive cortical regions compared to neutral facial stimuli. The ERPs to liked or disliked faces associated with normally distributed ratings (see below) were used to exclude the possibility that putative early modulations were caused by systematic low-level visual differences between stimulus sets rather than by affect. Accordingly, if indeed differences between liked and disliked faces did exist with respect to some uncontrolled physical characteristics (e.g., facial asymmetry, contrast, brightness), these confounds would equally contribute to the activity elicited by liked and disliked faces. All ERP data were digitally bandpass-filtered between 1.5 and 30 Hz.

To address possible individual differences in N170 latency (Watanabe *et al.,* 1999; Rossion *et al.,* 2000), the latency and amplitude of the well-characterized face-sensitive N170 component were individually defined for each subject and condition. For the LORETA analyses, the N170 component was defined as the time point with maximal global field power (GFP) value (Lehmann and Skrandies, 1980) between 120 and 240 ms showing the characteristic N170 field configuration (roughly bilateral negativity over the posterior regions and positivity over the frontal regions). GFP is reference-free and was computed as the spatial standard deviation of the brain electrical field; it thus reflects brain activity across the entire scalp. GFP peaks index time points that likely reflect maximal activity of the neuronal populations. Without exception, the latency and amplitude of the N170 evoked by liked and disliked faces were unambiguously identified in every subject by a trained assistant blind to the experimental conditions.

LORETA Analyses

At the individually determined latencies (maximal GFP value between 120 and 240 ms), the cortical three-dimensional distribution of current density for liked, neutral, and disliked faces and the checkerboard-reversal stimuli was computed using LORETA (Pascual-Marqui *et al.,* 1994, 1999). The LORETA algorithm solves the inverse problem by assuming related orientations and strengths of neighboring neuronal sources (however, without assuming a specific number of generating sources). The core assumption of the algorithm—which is generally well supported by animal single-unit record-

ings (Pascual-Marqui *et al.,* 1994)—is mathematically implemented by finding the "smoothest" of all possible activity distributions.

The fact that the LORETA algorithm does not assume a specific number of generating sources to solve the inverse problem is especially attractive in light of recent evidence gathered from intracranial ERP recordings suggesting that there may be two separate sources of face-sensitive activity approximately 200 ms poststimulus, one in the FG and one in the lateral occipitotemporal cortex (Allison *et al.,* 1999; McCarthy *et al.,* 1999; Puce *et al.,* 1999). Whereas other source localization techniques (e.g., equivalent dipole modeling) require *a priori* specification of the number of generating sources, detecting two sources that are separated spatially but not temporally is an inherent capacity of LORETA, as long as the sources are spatially separated by at least by 7–14 mm (Pascual-Marqui, 1999), as would be the case for the FG and lateral occipitotemporal cortex. Accordingly, if around 170–200 ms poststimulus a second face-sensitive source is indeed active, then the modeled LORETA activation in the FG would be adjusted by the presence of this second source. Since the FG has been the region most implicated in structural face encoding in functional neuroimaging studies (and for which coordinates of the face-sensitive voxels have been most consistently reported in the literature), main analyses were restricted to the FG. However, since a generating source located in the lateral occipitotemporal cortex could feasibly give rise to an N170 component, LORETA activity was also extracted and analyzed for the lateral occipitotemporal regions.

The version of LORETA employed here (Koles *et al.,* 2001; Mulert *et al.,* 2001; Pascual-Marqui *et al.,* 1999; Pizzagalli *et al.,* 2000, 2001) used a three-shell spherical head model registered to a standardized stereotactic space (Talairach and Tournoux, 1988) available as digitized MRI from the Brain Imaging Centre (Montreal Neurologic Institute, MNI305) and EEG electrode coordinates achieved using cross-registrations between spherical and realistic head geometry (Towle *et al.,* 1993). Computations were restricted to cortical gray matter and hippocampi according to the digitized Probability Atlases also available from the Brain Imaging Centre (Montreal Neurologic Institute). A voxel was labeled as gray matter if its probability of being gray matter (a) exceeded 33%, (b) exceeded the probability of being white matter, and (c) exceeded the probability of being cerebrospinal fluid. In the current implementation, a spatial resolution of 7 mm is realized (2394 voxels). At each voxel, current density was computed as the linear, weighted sum of the scalp electric potentials and subsequently log-transformed to normalize the distribution. LORETA units are scaled to amperes per square meter (A/m^2).

At the N170 latency, mean activity was extracted for the FG, the main region that has been implicated in structural encoding of faces in functional neuroimaging studies. The FG region-of-interest (ROI) was defined according to two complementary strategies: (1) use of Structure-Probability Maps (Lancaster *et al.,* 1997) and (2) use of coordinates of the voxel with the strongest face-sensitive response derived separately from each of five published fMRI studies (Puce *et al.,* 1996; Kanwisher *et al.,* 1997; McCarthy *et al.,* 1997; Aguirre *et al.,* 1999; Haxby *et al.,* 1999). Specifically, the ROI was defined as the meta-cluster common to three or more of the five fMRI studies. These studies were included because they specifically investigated face recognition and they utilized methods with the best available spatial resolution.

For the first strategy, activity was separately averaged for each hemisphere at voxels that according to the Structure-Probability Maps (Lancaster *et al.,* 1997) belong to the FG. For the second strategy, due to the low spatial resolution of our method, it was not always possible to find a LORETA voxel exactly matching the peak reported in the fMRI studies. To circumvent this limitation, LORETA activity was extracted from either (a) a single voxel that was closest to the fMRI coordinates or (b) a cluster whose center of gravity was closer than any possible single LORETA voxel to the fMRI coordinates. These solutions minimized the difference vectors between the original fMRI coordinates and the LORETA voxel or center of gravity. Subsequently, activity was averaged separately for each hemisphere from those voxels common to three or more of the five fMRI studies mentioned above. Table 1 and Fig. 1 and 2 show the coordinates and spatial extent of the ROIs defined according to each strategy.

For the lateral occipitotemporal cortex, the only face-sensitive coordinates available were those reported by Puce *et al.* (1996); thus, LORETA activity was extracted using their coordinates (X = 43, Y = −65, Z = −4). This face-sensitive, right-hemispheric region was approximated by a LORETA cluster at X = 44.30 ± 3.50, Y = −65.30 ± 3.50, Z = −6.00 ± 5.70 (four voxels). For each ROI, the LORETA activity was logarithmically transformed for normalization of the distribution.

Conventional Scalp ERP Waveform Analyses

For better comparison between the present and prior ERP studies employing conventional ERP waveform analyses, scalp ERP waveforms (reference: Fpz) were analyzed with respect to latency and amplitude of the N170 at posterior electrodes (T7/8, P7/8, P3/4, PO1/2, and O1/2). For each subject and condition, the N170 was identified at each electrode as the most negative deflection within 120 and 240 ms poststimulus.

TABLE 1

Summary of Fusiform Gyrus (FG) Regions-of-Interest (ROI) Entered in the Analyses

	ROI source	Side	fMRI studies[a]			LORETA approximation[b]			Voxels	Vector[c]	BA
			X	Y	Z	X	Y	Z			
A	LORETA	right	N/A	N/A	N/A	43.50 (8.19)	−54.00 (15.3)	−15.00 (3.06)	17	N/A	19/20/37
		left	N/A	N/A	N/A	−42.00 (8.21)	−56.00 (15.9)	−14.00 (2.93)	19	N/A	19/20/36/37
B	Aguirre	right	37	−62	−17	37.30 (3.50)	−60.00 (5.70)	−16.50 (4.00)	4	2.08	19/37
	Haxby	right	39	−59	−16	39.00 (0.00)	−60.00 (0.00)	−16.50 (4.95)	2	1.12	37
		left	−39	−55	−23	−41.50 (4.04)	−54.75 (6.70)	−21.75 (3.50)	4	2.81	36/37
	Kanwisher	right	40	−55	−10	40.75 (6.70)	−54.75 (3.50)	−9.50 (4.04)	4	0.94	37
		left	−35	−63	−10	−35.20 (7.98)	−62.80 (6.26)	−10.20 (3.83)	5	0.35	19/37
	McCarthy	right	36	−52	−19	35.50 (4.90)	53.00 (0.00)	−20.00 (0.00)	2	1.50	37
		left	−35	−56	−17	−34.50 (4.04)	−56.50 (4.04)	−16.50 (4.04)	4	0.87	37
	Puce	right	31	−54	−21	32.00 (0.00)	−53.00 (0.00)	−20.00 (0.00)	1	1.73	37
		left	−39	−54	−23	−38.00 (0.00)	−53.00 (0.00)	−20.00 (0.00)	1	3.32	37
C	Meta-cluster	right	N/A	N/A	N/A	37.25 (3.50)	−60.00 (5.72)	−16.50 (4.04)	4	N/A	19/37
		left	N/A	N/A	N/A	−38.00 (0.00)	−56.50 (4.95)	−20.00 (0.00)	2	N/A	37

Note. The FG ROIs were defined by (A) the Structure-Probability Maps, (B) the coordinates of prior fMRI studies, and (C) the meta-cluster common to the majority of these studies. Brodmann areas (BA) of the LORETA voxels used for the analyses are reported (Lancaster *et al.,* 1997). Coordinates in mm (Talairach and Tournoux, 1988). Origin at anterior commissure; (X) = left(−) to right(+); (Y) = posterior(−) to anterior(+); (Z) = inferior(−) to superior(+).

[a] Original coordinates reported in the single fMRI studies (Puce *et al.,* 1996: Faces vs texture subtraction; Kanwisher *et al.,* 1997; McCarthy *et al.,* 1997: Faces vs objects subtraction; Aguirre *et al.,* 1999; Haxby *et al.,* 1999).

[b] Mean coordinates (and SD) of LORETA's center of gravity of the cluster minimizing the distance (Vector;[c] see also *Materials and Methods*) between the original fMRI and the LORETA coordinates.

Statistical Analyses

Due to missing data for various reasons (see Results), only 13 subjects had ERPs under all four conditions. Consequently, to increase statistical power, main analyses compared ERP data for liked and disliked faces only ($n = 17$). However, to test the functional specificity of putative results, additional analyses including control stimuli were performed.

For the scalp N170 GFP and latency, separate paired Student's *t* tests were computed to assess differences between liked and disliked faces. For the scalp ERP waveforms, separate ANOVAs were run on the N170 amplitudes and latencies data using *Affect* (liked faces, disliked faces), *Electrodes* (T7/8, P7/8, P3/4, PO1/2, O1/2), and *Hemisphere* (left, right) as repeated measures. For the LORETA analyses, for each strategy, the extracted N170 activity was entered into a two-way ANOVA with *Affect* (liked faces, disliked faces) and *Hemisphere* (left, right) as repeated measures. To test the consistency of the results across subjects, binomial statistics were used to assess whether the number of subjects showing a given pattern of results differed from chance; binomial probabilities for B (17, 0.5) are reported.

For the additional analyses involving the control ERPs, separate one-way ANOVAs were performed for the N170 GFP and latency with a three-level *Condition* factor (liked, disliked, and checkerboard-reversal stimuli or neutral faces) as repeated measure. For the LORETA data, a two-way ANOVA with *Condition*

(liked faces, disliked faces, checkerboard-reversal stimuli *or* neutral faces) and *Hemisphere* (left, right) as repeated measures was run using the FG definition according to the Structure-Probability Maps. Overall, when violations of sphericity occurred (i.e., when the assumption of equality of variances of the differences between conditions was violated), the Greenhouse–Geisser correction was applied. Paired *t* tests were used as post hoc tests. Throughout, two-tailed *P* values are reported. Partial η^2 values were computed to assess the effect size of significant results (Tabachnick and Fidell, 1996).

Finally, in addition to the hypothesis-driven ROI approach targeting the face-sensitive ROIs, a separate whole-brain analysis using voxelwise paired *t* tests examined differences between liked and disliked faces at the individually assessed N170 latencies. The results are presented at $P < 0.05$, corrected for multiple comparisons (Holmes *et al.,* 1996). The Structure-Probability Maps atlas (Lancaster *et al.,* 1997) was used to label regions and Brodmann areas (Brodmann, 1909) showing significant differences between liked and disliked faces.

RESULTS

Postrecording Affective Ratings

One female participant was omitted from the analyses because her affective ratings were so negatively biased that it was not possible to compute the ERPs for
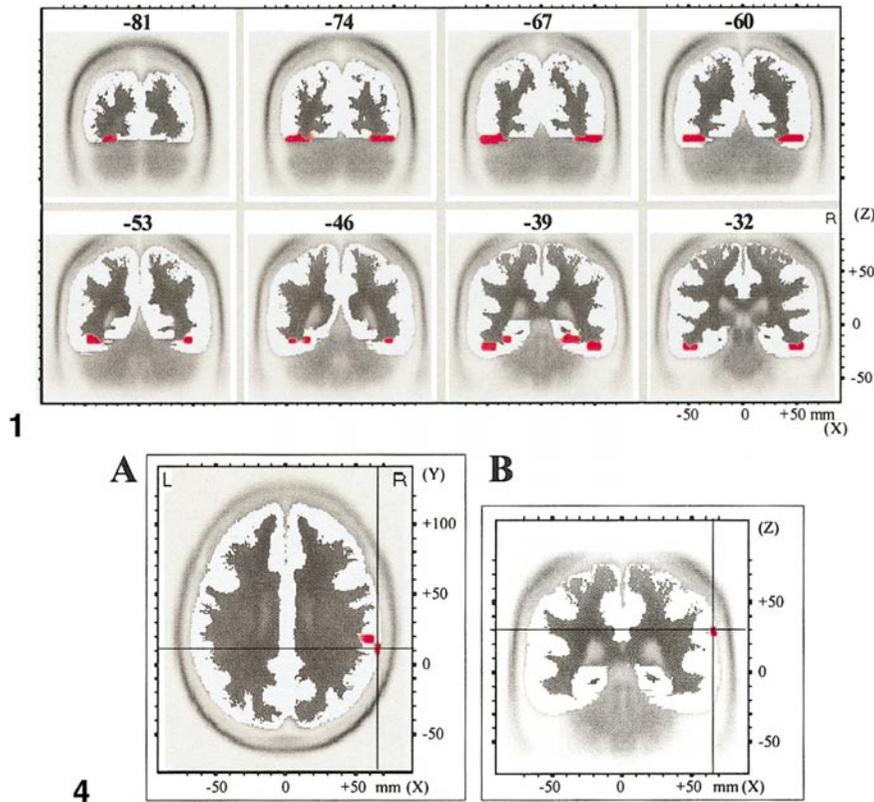
FIG. 1. Coronal slices (from y = −81, most posterior, to y = −32, most anterior) showing the location and spatial extent of (and not the activation level in) the FG cluster (red) as defined by the Structure-Probability Maps (Lancaster *et al.,* 1997). Origin at anterior commissure; (X) = left(−) to right(+); (Y) = posterior(−) to anterior(+); (Z) = inferior(−) to superior(+). In Figs. 1 and 2, the right hemisphere is shown on the right-hand side.

FIG. 4. Results of the whole-brain LORETA analysis run in addition to the hypothesis-driven ROI approach comparing disliked vs liked faces in the entire brain volume. Axial (*A*) and coronal (*B*) slices are shown at the level of the maximal differences between liked and disliked face ($P < 0.05$, corrected for multiple comparisons). The cross hairs show the location of the extreme *t*-value [X = 67, Y = −39, Z = 29; $t(16) = −4.28$, $P < 0.05$] in the right supramarginal gyrus (BA 40), where liked faces elicited stronger activity than disliked faces. Coordinates in millimeters (Talairach and Tournoux, 1988).

liked faces (M = 1.68, SD = 1.46, possible range 0–10). For the remaining 17 subjects, the mean affective ratings for the 10 most liked and disliked faces were 8.18 (SD = 0.77, range 6.76–9.60) and 1.51 (SD = 0.81, range 0.39–3.10), respectively. To address the issue of individual differences in affective judgments, the distribution of the affective ratings across subjects was examined. Remarkably, 20 of the 32 stimuli (62.5%) had normally distributed ratings centered on the midpoint of the rating scale, as assessed with the Shapiro–Wilk test. Across subjects, among the subset of stimuli used to compute ERPs, at least half had normally distributed ratings (liked: 5.82/10; disliked: 5/10).

To test whether male and female participants equally liked male and female portraits, an ANOVA with *Gender of Participant* as between-subject factor and *Gender of Portrait* as repeated measure was performed on the affective ratings. No significant effects, in particular no significant interaction [$F(1,15) = 0.62$, $P > 0.45$], emerged.

The results of the behavioral study performed at the University of Wisconsin-Madison confirmed the result of the original sample by showing that 21 stimuli had normally distributed ratings centered on the midpoint of the rating scale (Shapiro–Wilk test). When considering the 32 faces, the mean like/dislike ratings (across subjects) for the two independent subject samples were highly correlated (Pearson's $r = 0.76$, $P < 0.001$). As listed in Table 2, on average, the faces were judged as having particularly low scores with respect to ratings of different facial expressions. Like/dislike and attractiveness ratings were proportionally higher, but on average were also below the midpoint of the scales. On a single-subject level, Pearson correlations were computed between like/dislike ratings and the other seven ratings across the 32 faces. Binomial tests revealed significant results for the happiness and attractiveness ratings only: for these two ratings, at least 18 of the 23 subjects [$P(18/23) < 0.015$] showed positive cor-
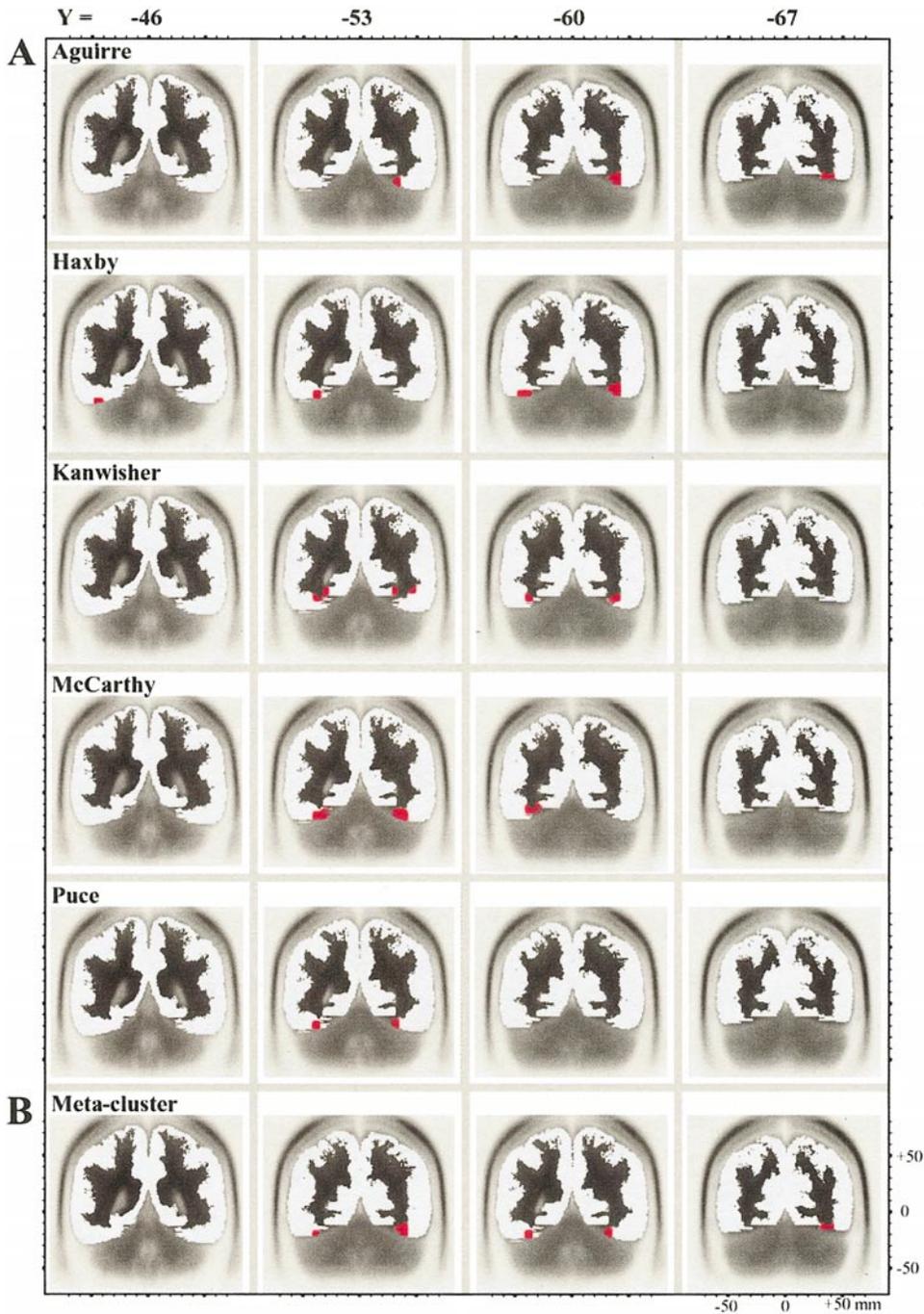
FIG. 2. Coronal slices (from y = −67, most posterior, to y = −46, most anterior) showing the location and spatial extent of (and not the activation level in) the fusiform gyrus in LORETA space. All voxels needed to approximate the face-sensitive fMRI coordinates through interpolation are shown. (A) ROIs defined by the coordinates of prior fMRI studies (Puce *et al.,* 1996; Kanwisher *et al.,* 1997; McCarthy *et al.,* 1997; Aguirre *et al.,* 1999; Haxby *et al.,* 1999); (B) ROIs defined by the meta-cluster common to prior fMRI studies.

relations at a nominal $P < 0.05$ (Pearson's $r >$ 0.349) with like/dislike ratings. At $P < 0.01$ ($r >$ 0.449), only attractiveness showed significant results (17 of the 23 subjects showed positive correlations with like ratings).

Scalp N170 GFP

The mean GFP latency of the N170 was virtually identical for liked (158.12 ± 9.39 ms, range 136–172) and disliked (158.59 ± 9.27 ms, range 136–172) faces

TABLE 2

Affective Rating Data Collected in an Independent Subject Sample ($n = 23$) Not Participating in the ERP Study

Affective term	Scale	Mean	SD	Min. mean	Max. mean
Like/dislike	0–10	4.43	0.95	2.47	6.06
Fear	0–6	1.40	0.97	0.06	3.09
Anger	0–6	1.80	0.75	0.47	3.13
Surprise	0–6	1.16	0.73	0.13	2.47
Happiness	0–6	1.65	0.60	0.69	2.88
Disgust	0–6	1.69	1.00	0.19	3.72
Sadness	0–6	2.05	0.79	0.72	3.47
Attractiveness	0–10	3.57	1.08	1.38	5.47

[$t(16) = 1.0$, $P > 0.30$]. Compared to disliked, liked faces elicited a stronger N170 GFP [4.47 ± 1.10 μV vs 4.30 ± 1.07 μV, $t(16) = 3.42$, $P < 0.005$, $\eta^2 = 0.42$]. Liked faces elicited greater N170 GFP compared to disliked faces in 14 of the 17 subjects [binomial $P(14/17) < 0.01$].[2]

Scalp ERP Waveform Analyses

A three-way ANOVA with *Affect* (liked faces, disliked faces), *Electrodes* (T7/8, P3/4, P7/8, PO3/4, O1/2), and *Hemisphere* (left, right) tested for possible N170 amplitude and latency differences for the two facial stimuli. For N170 amplitudes, significant results included the main effect of *Affect* [liked: -6.18 μV < disliked: -5.94 μV; $F(1,16) = 11.64$, $P < 0.005$, $\eta^2 = 0.42$], *Hemisphere* [right: -6.71 μV < left: -5.40 μV; $F(1,16) = 12.40$, $P < 0.005$, $\eta^2 = 0.44$], and *Electrodes* [$F(4,64) = 61.76$, $\varepsilon = 0.449$, $P < 0.001$, $\eta^2 = 0.79$] and a *Hemisphere* x *Electrodes* interaction [$F(4,64) = 5.33$, $\varepsilon = 0.647$, $P < 0.005$, $\eta^2 = 0.25$]. Planned comparisons showed that liked faces evoked significantly stronger N170 amplitudes over bilateral occipitoparietal regions (P7/8, O1/2; all Ps < 0.01; Fig. 3). At these electrodes, liked faces elicited greater N170 compared to disliked faces in at least 13 of the 17 subjects [binomial $P(13/17) < 0.05$]. A similar three-way ANOVA run on the N170 latency at the various electrodes revealed no significant effects.

In light of recent results suggesting that affect-modulated brain electrical activity can occur very early (<120 ms) in the human brain (Pizzagalli *et al.,* 1999; Halgren *et al.,* 2000), an additional analysis investigated whether ERP differentiation between liked and disliked faces may occur before the N170 component. To identify putative differences between liked and dis-

liked faces at short latencies, paired *t* tests were computed for each time frame between 60 and 180 ms at T7/8, P3/4, P7/8, PO3/4, and O1/2. This strategy has proven powerful in recent cases of early task-related ERP modulations not confined to a given component (Braeutigam *et al.,* 2001; VanRullen and Thorpe, 2001). To address the issue of multiple comparisons, differences between liked and disliked faces were considered significant only if (a) at least five consecutive *t* test values were below the $P < 0.05$ level and (b) at least 12 of the 17 subjects [binomial $P(12/17) < 0.05$] showed such modulation at each time frame. According to these criteria, significant differences between liked and disliked faces that preceded the N170 peak emerged at O2 (116–156 ms, 11 consecutive time frames; P100: dislike > like; N170: like > dislike), P8 (112–128 ms, 5 time frames; P100: dislike > like), O1 (140–160 ms, 6 time frames; N170: like > dislike), and P7 (140–164 ms, 7 time frames; N170: like > dislike); see also Fig. 3.

ROIs Defined by the Structure-Probability Maps

The ANOVA revealed a significant main effect of *Affect* [$F(1,16) = 5.65$, $P < 0.05$, $\eta^2 = 0.26$] and *Hemisphere* [$F(1,16) = 14.27$, $P < 0.001$, $\eta^2 = 0.47$]. Liked faces evoked significantly stronger bilateral FG activity than disliked faces ($+4.65\%$; -2.16 ± 0.15 A/m² vs -2.18 ± 0.14 A/m²).[3] This modulation was present in 12 of the 17 subjects [binomial $P(12/17) < 0.05$]. Overall, stimuli elicited significantly stronger activity in the right compared to the left hemisphere ($+31.03\%$; -2.11 ± 0.18 A/m² vs -2.23 ± 0.13 A/m²). See Fig. 1 and Table 1A.

ROIs Defined by the Meta-Cluster Common to Prior fMRI Studies

This ANOVA revealed only a significant main effect of *Affect* [$F(1,16) = 5.37$, $P < 0.05$, $\eta^2 = 0.25$] such that liked faces were associated with significantly stronger bilateral FG activity than disliked faces ($+4.25\%$; -2.25 ± 0.16 A/m² vs -2.27 ± 0.16 A/m²). This modulation was present in 12 of the 17 subjects [binomial $P(12/17) < 0.05$]. See Fig. 2 and Table 1C.

Whole-Brain LORETA Analysis

The whole-brain analysis run in addition to the hypothesis-driven ROI approach at the individually assessed N170 latencies revealed that liked faces evoked stronger activity than disliked faces in the right parietal lobe centered on the supramarginal gyrus (SMG; BA 40, X = 67, Y = −39, Z = 29, $t(16) = -4.28$,

---

[2] Following a reviewer's request, these analyses were repeated using unfiltered ERPs. The result of greater GFP for liked than disliked faces was confirmed ($P < 0.05$). For a better signal extraction from the background noise, remaining analyses were performed on the filtered ERPs.

[3] LORETA results are negative because they were log-transformed for normalization purposes. Less negative values reflect higher current density.
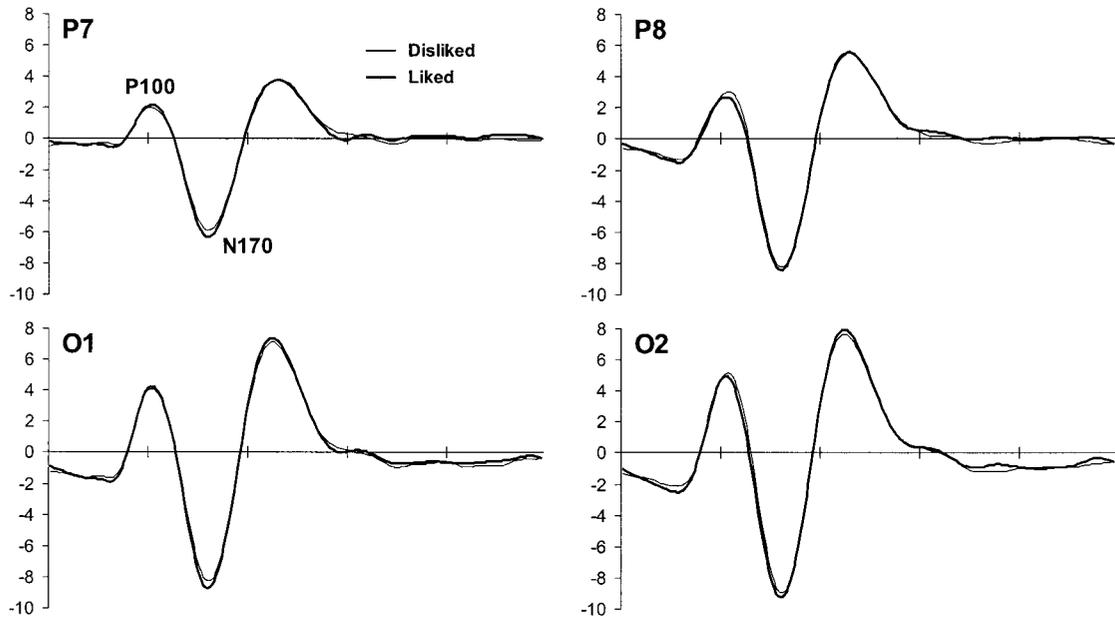
FIG. 3. Grand mean ERP (*n* = 17) waveforms evoked by liked (thick lines) and disliked (thin lines) faces at P7, P8, O1, and O2. Horizontal: time in milliseconds (from 0 to 500 ms poststimulus); vertical: amplitude in microvolts. At P7, the P100 and N170 components are shown.

corrected *P* < 0.05). At these voxels, increased activity for liked faces (+9.26%) was observed in 16 of the 17 subjects [binomial *P*(16/17) < 0.001]. See Fig. 4.

Correlation between FG and Right Parietal Region

Pearson's correlations were used to assess the covariance between affect-modulated activity in the right SMG and FG activity. Difference scores (liked-minus-disliked) for the right SMG and FG activity (according to the Structure-Probability Maps and the meta-cluster common to prior fMRI studies) were computed and correlated. Irrespective of FG definition, the scores were significantly positively correlated in the right (*r* = 0.52–0.54, *P* < 0.05), but not the left (*r* = 0.21–0.34, *P* > 0.18) FG. Thus, the greater the affect modulation in the right SMG, the greater the modulation in the FG. It should be noted that the correlations involving the left and right FG were not significantly different. The difference scores for the left and right FG were not significantly correlated (Structure-Probability Maps: *r* = 0.44, *P* = 0.08; meta-cluster; *r* = 0.34, *P* > 0.15). See Fig. 5.

Additional Analyses

Checkerboard-reversals as control stimuli. Only 14 of the 17 subjects showed a reliable (though strongly attenuated) N170 GFP peak (main effect of *Condition*: $F_{(2,26)}$ = 158.54, ε = 0.542, *P* < 0.001, η^2 = 0.92; liked faces: 4.42 ± 1.04 μV > disliked faces: 4.26 ± 1.01 μV > checkerboard-reversal stimuli: 1.08 ± 0.39 μV; all

*P*s < 0.05). For the LORETA analyses, the main effects of both *Condition* [$F_{(2,26)}$ = 6.22, ε = 0.489, *P* < 0.05, η^2 = 0.32] and *Hemisphere* [$F_{(1,13)}$ = 4.82, *P* < 0.05, η^2 = 0.27] were significant. Post hoc tests showed that liked faces (−2.18 ± 0.15 A/m²) elicited stronger FG activity compared to both disliked faces (−2.20 ± 0.14 A/m²) and checkerboard-reversal stimuli (−2.39 ± 0.22 A/m²), which in turn differed from each other (all pairwise comparisons, *P* < 0.05). Further, the main effect of *Hemisphere* was due to higher FG activity in the
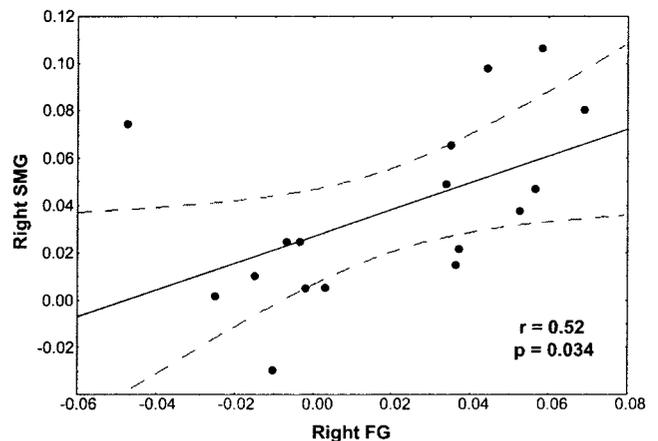

FIG. 5. Pearson's correlation between differential activity (liked-minus-disliked) within the right supramarginal gyrus (y axis) and the right FG (x axis). FG cluster defined by the meta-cluster common to prior fMRI studies. Units scaled to A/m². Dotted lines: ±95% confidence intervals.

right (-2.21 ± 0.17 A/m^2) than in the left (-2.31 ± 0.07 A/m^2) hemisphere.

Neutral faces as control stimuli. Three subjects were excluded from these analyses because of either no available ratings between 4.5 and 5.5 on the analog scale (two subjects) or an insufficient number of artifact-free epochs (one subject). For both the N170 GFP peak and the N170 latency, the main effect of *Condition* (liked faces, disliked faces, neutral faces) was significant or approached significance [GFP: $F(2,26) = 2.90$, $\varepsilon = 0.687$, $P = 0.096$, $\eta^2 = 0.22$; latency: $F(2,26) = 7.72$, $\varepsilon = 0.800$, $P < 0.005$, $\eta^2 = 0.37$]. Post hoc tests revealed that liked faces (4.43 ± 1.06 μV) had higher GFP than both disliked faces (4.24 ± 0.98 μV; $t(13) = 3.55$, $P < 0.005$) and neutral faces (4.23 ± 1.17 μV; $t(13) = 1.90$, $P = 0.08$). Both liked (158.00 ± 10.26 ms; $P < 0.05$) and disliked (158.29 ± 10.13 ms; $P < 0.05$) faces elicited earlier N170 than neutral faces (160.57 ± 8.72 ms). For the LORETA data, the two-way ANOVA revealed a significant main effect of *Hemisphere* [$F(1,13) = 6.47$, $P < 0.05$, $\eta^2 = 0.33$] and a statistical trend for the main effect of *Condition* [$F(2,26) = 3.31$, $\varepsilon = 0.801$, $P = 0.052$, $\eta^2 = 0.20$]. Liked faces ($-2.15 + 0.13$ A/m^2) tended to elicit stronger activation in the FG compared to both disliked ($-2.17 + 0.11$ A/m^2; $P = 0.07$) and neutral ($-2.18 + 0.15$ A/m^2; $P = 0.052$) faces.

Liked or disliked faces with normally distributed ratings. Despite lower signal-to-noise ratio [(number of artifact-free epochs) liked: 91.42 ± 30.08 vs disliked: 102.11 ± 25.62; not significant], this analysis revealed a significant main effect of *Hemisphere* [right > left, $F(1,16) = 18.98$, $P < 0.0005$, $\eta^2 = 0.54$] and, more importantly, a significant *Affect × Hemisphere* interaction [$F(1,16) = 4.71$, $P < 0.05$, $\eta^2 = 0.23$]. Post hoc tests revealed that, compared to disliked faces, liked faces elicited stronger activity in the right [-2.08 ± 0.18 A/m^2 vs -2.10 ± 0.18 A/m^2; $t(16) = -2.18$, $P < 0.05$] but not left [-2.23 ± 0.15 A/m^2 vs -2.22 ± 0.12 A/m^2; $t(16) = 0.96$, $P > 0.35$] FG.

Lateral occipitotemporal cortex as possible generating source for N170. A paired *t* test contrasted activity elicited by liked and disliked faces at voxels that approximate the coordinates reported by Puce *et al.* (1996) as being face sensitive. At these LORETA voxels, liked faces elicited stronger activation than disliked faces ($+5.44\%$; -1.88 ± 0.21 A/m^2 vs -1.90 ± 0.22 A/m^2; $t(16) = 2.42$, $P < 0.05$, $\eta^2 = 0.27$).

DISCUSSION

The present results can be summarized as follows. First, scalp-recorded ERPs and cortical current density peaking $\sim$160 ms poststimulus within the FG (and lateral occipitotemporal) regions reliably covaried with self-reported liking judgments. Second, liked faces were associated with greatest activity in the right pa-

rietal lobe. Third, affect-modulated activity within the right SMG and right FG was positively correlated. Fourth, facial stimuli evoked stronger activity in the right compared to the left hemisphere. Fifth, affect-laden stimuli evoked stronger activity at the scalp (N170 GFP) and within the FG compared to control stimuli (neutral faces and checkerboard-reversal stimuli). Finally, affect-modulated brain electrical activity appeared over posterior regions earlier than the N170 peak ($\sim$112 ms). By combining information gathered from functional neuroimaging studies with the excellent temporal resolution of ERP data, the present results demonstrate that structural face encoding occurring within the FG 160 ms poststimulus can be influenced by affective features conveyed by faces.

Methodological Considerations

It is important to briefly emphasize several methodological features of this research. First, to address possible individual variability in N170 latency (Watanabe *et al.,* 1999; Rossion *et al.,* 2000), its latency was assessed individually. Second, to account for large individual differences in affective judgments, ERPs were computed with individually assessed affective ratings. Notably, in both the ERP and the behavioral studies, more than 60% of the stimuli had normally distributed ratings centered on the midpoint, confirming the necessity of considering large individual differences in neuroscientific investigations of affect (Davidson and Irwin, 1999; Pizzagalli *et al.,* 1999), particularly when using ambiguous stimuli. Failure to account for such differences would have greatly reduced the power of our analyses and thus the ability to observe these lawful relations. Notably, when reanalyzing the ERPs with only those stimuli showing normally distributed affective ratings, the affect-modulated activity in the FG was still present. These results are especially important because they exclude the possibility that the affective modulations starting at 112 ms and the one at the N170 peak were related to physical or structural information embedded in the facial stimuli (see Pizzagalli *et al.,* 1999, for an independent demonstration of early affect-modulated activity not caused by physical stimulus features). In other words, they eliminate the possibility that the idiosyncratic affective judgments were based on configurations of physical features that are processed during structural encoding and that may lead to an early ERP differentiation, which may precede ERP modulations associated with affective judgment. In fact, a closer chronometrical analysis of the ERPs at posterior electrodes revealed that reliable differentiations between liked and disliked faces started *before* the N170 occurrence (112–160 ms), replicating recent findings (Halgren *et al.,* 2000; Pizzagalli *et al.,* 1999). From these and prior findings and from the independent behavioral results showing that the stim-

uli were not biased toward particular facial expressions, it seems parsimonious to conclude that affective processing rather than simple feature detection was responsible for the effects observed. A similar conclusion cannot be drawn from a recent ERP study that reported results in apparent contrast with the present findings (Halit *et al.,* 2000). Indeed, their finding of stronger N170 for unattractive, but at the same time, *atypical* faces may be in part due to differences in low-level features between unattractive (atypical) and attractive (typical) faces.

Third, a novel tomographic source localization technique free from a priori assumptions about the number of sources was employed. Previous studies employing LORETA have demonstrated that it provides physiologically meaningful results during basic visual and auditory tasks (Pascual-Marqui *et al.,* 1994) and cognitive tasks known to engage specific brain regions (Koles *et al.,* 2001; Mulert *et al.,* 2001; Pizzagalli *et al.,* 2000; Yamaguchi *et al.,* 2000). Particularly, recent studies from three independent groups furnished important cross-modal validation for LORETA. In a case study, LORETA generators of epileptogenic discharges could be confirmed by the locations of blood oxygenation level-dependent signal increase, as assessed with EEG-triggered fMRI and electrocorticography from subdural electrodes (Seeck *et al.,* 1998). Similarly, Worrell *et al.* (2000) found that LORETA generators of ictal discharge were very close to the locations of MRI-identified epileptic foci. Finally, we (Pizzagalli *et al.,* 2001) recently observed that treatment response in depression was predicted by LORETA activity within a region of the rostral anterior cingulate cortex, which was similar to the one previously reported in positron emission tomography (PET) studies on this topic (e.g., Mayberg *et al.,* 1997). In the present study, the utility of this technique was further enhanced by the use of prior fMRI results to guide and sharpen the analyses.

Despite these encouraging results, it is clear that an important limitation of the present study is the relatively low spatial resolution, which in some cases required relatively extended ROIs to approximate the fMRI coordinates. A second limitation is that only two classes of control stimuli were used to address the functional specificity of the N170 (neutral faces and checkerboard-reversal stimuli). Clearly, because checkerboard stimuli radically differed in their physical characteristics compared to facial stimuli, they were not optimal for testing the extent to which the N170 in this study was face specific. Given this limitation, we avoided a description of the current findings as being face-specific but preferred instead to consider them face-sensitive. Future research should utilize a larger range of control stimuli (e.g., houses, cars, hands), as recently proposed (Allison *et al.,* 1999; McCarthy *et al.,* 1999; Puce *et al.,* 1999; Halgren *et al.,* 2000; Kanwisher *et al.,* 1997; Liu *et al.,* 2000).

Affect-Modulated Activity in Face-Sensitive Regions

Incorporating results from prior ERP/MEG and fMRI studies and theoretical considerations, we predicted that affective ratings would covary with activity in face-sensitive regions prior to structural encoding completion (i.e., 170 ms). This was confirmed for both the FG and the lateral occipitotemporal cortex, two regions that have been most consistently proposed in the literature as possible neuronal generators for the face-sensitive N170 component. The finding that liked faces, which were rated as relatively more attractive by an independent subject sample, elicited stronger activity in these regions may reflect the behavioral observation that positively valenced and/or liked faces are recognized better/faster than negatively valenced and/or disliked faces (Kirouac and Dore, 1983; Bruce and McDonald, 1993; Esteves and Öhman, 1993; Kirita and Endo, 1995). Whereas the behavioral data suggested that affective information conveyed by faces can influence face recognition, the present results shed light on where and how these processes unfold in time. Note, however, that our results do not exclude the possibility that biologically fear-relevant stimuli (e.g., angry or fearful faces) may be processed more quickly and accurately (Öhman *et al.,* 2001) and thus may possibly evoke stronger FG activation. Since the stimuli used in the present study did not display strong facial expressions, future research should directly assess the effect of facial expressions on FG activation underlying the N170 component.

Our results have important implications for extant models of face recognition, particularly for the Bruce–Young model (1986), because they are incompatible with the proposal that affective features are necessarily extracted from faces only *after* the completion of structural encoding. Indeed, whereas prior scalp/intracranial ERP and MEG studies demonstrated that structural encoding occurs at ~170 ms poststimulus, recent studies have shown that activity occurring before 170 ms is modulated by affective facial features. For instance, in an independent study, we reported that self-reported affective judgments evoked different ERPs between 80 and 116 ms (Pizzagalli *et al.,* 1999). These findings were recently confirmed and extended by Halgren *et al.* (2000), who observed that activity occurring at 110 ms and modeled by a single dipole localized to the posterior-inferior occipital midline was affected by facial expression. Finally, a recent MEG study reported preliminary evidence that activity occurring at 163 ms and modeled by a dipole in the FG was greater for happy compared to disgusted or neutral expressions (LaNoue *et al.,* 2000). Together, these results suggest either that affect is preattentively ex-

tracted before structural encoding is complete or that structural encoding starts earlier than previously assumed. In the following section, possible mechanisms that may explain the present results are discussed.

In a recent review, Adolphs (2002) highlighted a key role of the occipitotemporal cortices, amygdala, orbitofrontal cortex, basal ganglia, and right parietal cortices in recognition of emotion in facial stimuli. For some of these regions, early categorization of socially relevant information has been demonstrated. For example, Marinkovic and colleagues (2000) reported categorization of faces vs objects at ~150 ms poststimulus in the right inferior frontal gyrus of an epileptic patient with depth electrodes. Similarly, neuronal discrimination between fearful and happy facial expressions was observed starting at 120 ms at electrodes implanted in the right ventromedial prefrontal cortex (Kawasaki et al., 2001). Finally, electrophysiological responses to facial stimuli have been observed in the human amygdala at ~120 ms (Halgren et al., 1994). Based on these findings, Adolphs (2002) concluded that presentation of an affectively laden stimulus triggers an initial feedforward information processing along occipital and temporal neocortices which leads to a coarse categorization of affect and facial expression within the first 100 ms. Similarly, we propose that cholinergic-mediated basal forebrain regions (e.g., nucleus accumbens, sublenticular extended amygdala) may be activated very quickly and tune subsequent activity in the visual cortices subserving face processing through a mechanism of increased vigilance and attention (Heimer, 2000; Sarter and Bruno, 2000; LeDoux, 2000). The present findings of greater liked than disliked activity may reflect neuronal processing biases in brain reward circuits (ventral striatum, particularly nucleus accumbens), which have been recently found to be activated by attractive faces (Aharon et al., 2001; Kampe et al., 2001). Although the present liked faces were rated as being more attractive in the independent behavioral study, we note that the range of the attractiveness ratings in the current study was rather narrow. Thus, future studies should assess whether subtle differences in facial attractiveness are sufficient for recruiting processing in basal forebrain regions. Independent of the mechanisms involved, which cannot be probed with scalp ERP recordings, the present findings suggest that although the construction of a detailed representation of a face may require approximately 170 ms, a rapid, likely coarse affective categorization can occur at earlier latencies. This might suggest the existence of perceptual pathways in parallel to pathways devoted to full structural face encoding. Finally, our results not only emphasize that the FG is sensitive to salient facial information, but, unlike fMRI and PET results, also exclude the possibility that this modulation occurs later in the information processing flow due to reentrant projections from brain structures encoding affective information.

Right Parietal Activation

An independent whole-brain analysis demonstrated that maximal differentiation between liked and disliked faces occurred in right parietal regions centered on the supramarginal gyrus. In agreement with interpretations of N170 modulations in terms of stimulus salience (Bentin et al., 1996; Puce et al., 2000), we interpret this result as suggesting that liked faces, in the present task, were attentionally more engaging and salient than disliked faces. Three lines of evidence justify this interpretation. First, the right parietal region maximally activated by liked faces belongs to the visual attentional network (Posner and Dehaene, 1994). Second, lesions in the right temporoparietal lobes have been associated with impaired emotional experience and arousal (Heller, 1993; Heilman, 1997). Specifically, right supramarginal lesions led to deficits in recognizing, labeling, and building conceptual knowledge about facial expressions (Adolphs et al., 2000). Third, functional neuroimaging studies have proposed that the right parietal lobe, and especially the right supramarginal gyrus, belongs to a network devoted to visual saliency detection. Socially relevant information, such as facial expression (Gur et al., 1994), eye gazes (Wicker et al., 1998), and one's own face (Sugiura et al., 2000) reliably activated these regions. As both FG (Wojciulik et al., 1998) and N170 (Lueschow et al., 2000) responses are stronger for attended faces, increased FG activation for liked faces may be interpreted in terms of enhanced attention and deeper encoding due to their saliency within the context of the present stimulus set, which in general received low ratings of attractiveness.

Hemispheric Differences

In the present study involving presentation of affectively laden facial stimuli, three findings emphasized a key role of the right hemisphere. First, the right FG was generally more activated than the left FG in response to the facial stimuli. Second, analyses involving stimuli with normally distributed ratings showed that liked faces elicited stronger activity than disliked faces in the right but not in the left FG. Third, the strongest like–dislike differentiation was observed in right parietal regions. Overall, these findings confirm a dominant role of right posterior regions in recognition of faces (e.g., Benton, 1990) and perception of emotional information (e.g., Davidson, 1993).

CONCLUSIONS

The present results show that activity within the face-sensitive regions (FG and lateral occipitotemporal

cortex) occurring ~160 ms poststimulus can be systematically modulated by self-reported affective ratings of the stimuli. Notably, affect-modulated brain electrical activity started already at ~112 ms poststimulus. Correlational analyses further revealed that affect-modulated FG activity was associated with increased right parietal activity, possibly because of the salient and arousing nature of liked stimuli in the current experimental context. These results indicate that techniques with excellent time resolution can play a crucial role in testing theoretical models and shed important light on some of the temporal aspects of affective processing and its interactions with structural face encoding.

ACKNOWLEDGMENTS

REFERENCES

Adolphs, R. 2002. Neural systems for recognizing emotion. *Curr. Opin. Neurobiol.* **12:** 169–177.

Adolphs, R., Damasio, H., Tranel, D., Cooper, G., and Damasio, A. R. 2000. A role for the somatosensory cortices in the visual recognition of emotion as revealed by three-dimensional lesion mapping. *J. Neurosci.* **20:** 2683–2690.

Aguirre, G. K., Singh, R., and D'Esposito, M. 1999. Stimulus inversion and the responses of face and object-sensitive cortical areas. *NeuroReport* **10:** 189–194.

Aharon, T., Etcoff, N., Ariely, D., Chabris, C. F., O'Connor, E., and Breiter, H. C. 2001. Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron* **32:** 537–551.

Allison, T., Puce, A., Spencer, D. D., and McCarthy, G. 1999. Electrophysiological studies of human face perception. I: Potentials generated in occipitotemporal cortex by face and non-face stimuli. *Cereb. Cortex* **9:** 415–430.

Bentin, S., Allison, T., Puce, A., Perez, E., and McCarthy, G. 1996. Electrophysiological studies of face perception in humans. *J. Cogn. Neurosci.* **8:** 551–565.

Bentin, S., and Deouell, L. Y. 2000. Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cogn. Neuropsychol.* **17:** 35–54.

Benton, A. 1990. Facial recognition. *Cortex* **26:** 491–499.

Bradley, B. P., Mogg, K., Millar, N., Bonhamcarter, C., Fergusson, E., Jenkins, J., and Parr, M. 1997. Attentional biases for emotional faces. *Cogn. Emotion* **11:** 25–42.

Braeutigam, S., Baley, A. J., and Swithenby, S. J. 2001. Task-dependent early latency (30–60 ms) visual processing of human faces and other objects. *NeuroReport* **12:** 1531–1536.

Breiter, H. C., Etcoff, N. L., Whalen, P. J., Kennedy, W. A., Rauch, S. L., Buckner, R. L., Strauss, M. M., Hyman, S. E., and Rosen, B. R. 1996. Response and habituation of the human amygdala during visual processing of facial expression. *Neuron* **17:** 875–887.

Brodmann, K. 1909. *Localisation in the Cerebral Cortex.* Smith-Gordon, London.

Bruce, A. J., and McDonald, B. G. 1993. Face recognition as a function of judgements of likability/unlikability. *J. Gen. Psychol.* **120:** 451–462.

Bruce, V., and Young, A. 1986. Understanding face recognition. *Br. J. Psychol.* **77:** 305–327.

Critchley, H., Daly, E., Phillips, M., Brammer, M., Bullmore, E., Williams, S., Van-Amelsvoort, T., Robertson, D., David, A., and Murphy, D. 2000. Explicit and implicit neural mechanisms for processing of social information from facial expressions: A functional magnetic resonance imaging study. *Hum. Brain Mapp.* **9:** 93–105.

Davidson, R. J. 1993. Cerebral asymmetry and emotion: Conceptual and methodological conundrums. *Cogn. Emotion* **7:** 115–138.

Davidson, R. J., and Irwin, W. 1999. The functional neuroanatomy of emotion and affective style. *Trends Cogn. Sci.* **3:** 11–21.

Dolan, R. J., Fletcher, P., Morris, J., Kapur, N., Deakin, J. F., and Frith, C. D. 1996. Neural activation during covert processing of positive emotional facial expressions. *Neuroimage* **4:** 194–200.

Eimer, M. 2000. The face-specific N170 component reflects late stages in the structural encoding of faces. *NeuroReport* **11:** 2319–2324.

Esteves, F., and Oehman, A. 1993. Masking the face: Recognition of emotional facial expressions as a function of the parameters of backward masking. *Scand. J. Psychol.* **34:** 1–18.

George, N., Dolan, R. J., Fink, G. R., Baylis, G. C., Russell, C., and Driver J. 1999. Contrast polarity and face recognition in the human fusiform gyrus. *Nat. Neurosci.* **2:** 574–580.

Golby, A. J., Gabrieli, J. D. E., Chiao, J. Y., and Eberhardt, J. L. 2001. Differential responses in the fusiform region to same-race and other-race faces. *Nat. Neurosci.* **4:** 845–850.

Gur, R. C., Skolnick, B. E., and Gur, R. E. 1994. Effects of emotional discrimination tasks on cerebral blood flow: Regional activation and its relation to performance. *Brain Cogn.* **25:** 271–286.

Halgren, E., Baudena, P., Heit, G., Clarke, J. M., Marinkovic, K., and Clarke, M. 1994. Spatio-temporal stages in face and word processing. I. Depth-recorded potentials in the human occipital, temporal and parietal lobes. *J. Physiol. (Paris)* **88:** 1–50.

Halgren, E., Raij, T., Marinkovic, K., Jousmaeki, V., and Hari, R. 2000. Cognitive response profile of the human fusiform face area as determined by MEG. *Cereb. Cortex* **10:** 69–81.

Halit, H., de Haan, M., and Johnson, M. H. 2000. Modulation of event-related potentials by prototypical and atypical faces. *NeuroReport* **11:** 1871–1875.

Hariri, A. R., Bookheimer, S. Y., and Mazziotta, J. C. 2000. Modulating emotional responses: Effects of a neocortical network on the limbic system. *NeuroReport* **11:** 43–48.

Haxby, J. V., Hoffman, E. A., and Gobbini, M. I. 2000. The distributed human neural system for face perception. *Trends Cogn. Sci.* **4:** 223–233.

Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A., and Martin, A. 1999. The effect of face inversion on activity in human neural systems for face and object perception. *Neuron* **22:** 189–199.

Heilman, K. M. 1997. The neurobiology of emotional experience. *J. Neuropsychiatry Clin. Neurosci.* **9:** 439–448.

Heimer, L. 2000. Basal forebrain in the context of schizophrenia. *Brain Res. Brain Res. Rev.* **31:** 205–235.

Heller, W. 1993. Neuropsychological mechanisms of individual differences in emotion, personality, and arousal. *Neuropsychology* **7:** 476–489.

Holmes, A. P., Blair, R. C., Watson, J. D. G., and Ford, I. 1996. Non-parametric analysis of statistic images from functional mapping experiments. *J. Cereb. Blood Flow Metab.* **16:** 7–22.

Kampe, K. K. W., Frith, C. D., Dolan, R. J., and Frith, U. 2001. Reward value of attractiveness and gaze. *Nature* **413:** 589.

Kanwisher, N. 2000. Domain specificity in face perception. *Nat. Neurosci.* **3:** 759–763.

Kanwisher, N., McDermott, J., and Chun, M. M. 1997. The fusiform face area: A module in human extrastriate cortex specialized for face perception. *J. Neurosci.* **17:** 4302–4311.

Kawasaki, H., Adolphs, R., Kaufman, O., Damasio, H., Damasio, A. R., Granner, M., Bakken, H., Hori, T., and Howard, M. A. 2001. Single-neuron responses to emotional visual stimuli recorded in human ventral prefrontal cortex. *Nat. Neurosci.* **4:** 15–16.

Kirita, T., and Endo, M. 1995. Happy face advantage in recognizing facial expressions. *Acta Psychol.* **89:** 149–163.

Kirouac, G., and Dore, F. Y. 1983. Accuracy and latency of judgment of facial expressions of emotions. *Percept. Mot. Skills* **57:** 683–686.

Koles, Z. J., Flor-Henry, P., and Lind, J. C. 2001. Low-resolution electrical tomography of the brain during psychometrically matched verbal and spatial cognitive tasks. Hum. *Brain Mapp.* **12:** 144–156.

Kuskowski, M. A., and Pardo, J. V. 1999. The role of the fusiform gyrus in successful encoding of face stimuli. *NeuroImage* **9:** 599–610.

Lancaster, J. L., Rainey, L. H., Summerlin, J. L., Freitas, C. S., Fox, P. T., Evans, A. C., Toga, A. W., and Mazziotta, J. C. 1997. Automated labeling of the human brain—A preliminary report on the development and evaluation of a forward-transformed method. *Hum. Brain Mapp.* **5:** 238–242.

LaNoue, M. D., Edgar, C. J., and Weisend, M. P. 2000. Magnetoencephalographic correlates of the processing of emotional facial expressions. *J. Cogn. Neurosci. Suppl.* **S:** 70.

LeDoux, J. E. 2000. Emotion circuits in the brain. *Annu. Rev. Neurosci.* **23:** 155–184.

Lehmann, D., and Skrandies, W. 1980. Reference-free identification of components of checkerboard-evoked multichannel potential fields. *Electroencephalogr. Clin. Neurophysiol.* **48:** 609–621.

Liu, J., Higuchi, M., Marantz, A., and Kanwisher, N. 2000. The selectivity of the occipitotemporal M170 for faces. *NeuroReport* **11:** 337–341.

Lueschow, A., Sander, T., Boehm, S. G., Nolte, G., Trahms, L., Marx, P., and Curio, G. 2000. Attention modulates inferotemporal MEG/EEG activity differently for faces and houses. *J. Cogn. Neurosci. Suppl.* **S:** 92–93.

Marinkovic, K., Trebon, P., Chauvel, P., and Halgren, E. 2000. Localised face processing by the human prefrontal cortex: Face-selective intracerebral potentials and post-lesion deficits. *Cogn. Neuropsychol.* **17:** 187–199.

Mayberg, H. S., Brannan, S. K., Mahurin, R. K., Jerabek, P. A., Brickman, J. S., Tekell, J. L., Silva, J. A., McGinnis, S., Glass, T. G., Martin, C. C., and Fox, P. T. 1997. Cingulate function in depression: A potential predictor of treatment response. *NeuroReport* **8:** 1057–1061.

McCarthy, G., Puce, A., Belger, A., and Allison, T. 1999. Electrophysiological studies of human face perception. II: Response properties of face-specific potentials generated in occipitotemporal cortex. *Cereb. Cortex* **9:** 431–444.

McCarthy, G., Puce, A., Gore, J. C., and Allison, T. 1997. Face-specific processing in the human fusiform gyrus. *J. Cogn. Neurosci.* **9:** 605–610.

Morris, J. S., Friston, K. J., Buchel, C., Frith, C. D., Young, A. W., Calder, A. J., and Dolan, R. J. 1998. A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain* **121:** 47–57.

Mouchetant-Rostaing, Y., Giard, M. H., Bentin, S., Aguera, P. E., and Pernier, J. 2000. Neurophysiological correlates of face gender processing in humans. *Eur. J. Neurosci.* **12:** 303–310.

Mulert, C., Gallinat, J., Pascual-Marqui, R., Dorn, H., Frick, K., Schlattmann, P., Mientus, S., Herrmann, W. M., and Winterer, G. 2001. Reduced event-related current density in the anterior cingulate cortex in schizophrenia. *NeuroImage* **13:** 589–600.

Öhman, A., Lundqvist, D., and Esteves, F. 2001. The face in the crowd revisited: A threat advantage with schematic stimuli. *J. Pers. Soc. Psychol.* **80:** 381–396.

Oldfield, R. C. 1971. The assessment of handedness: The Edinburgh inventory. *Neuropsychologia* **9:** 97–113.

Pascual-Marqui, R. D. 1999. A review of methods for solving the EEG inverse problem. *Int. J. Bioelectromagnet.* **1:** 75–86.

Pascual-Marqui, R. D., Lehmann, D., Koenig, T., Kochi, K., Merlo, M. C. G., Hell, D., and Koukkou, M. 1999. Low resolution brain electromagnetic tomography (LORETA) functional imaging in acute, neuroleptic-naive, first-episode, productive schizophrenia. *Psychiatry Res. Neuroimag.* **90:** 169–179.

Pascual-Marqui, R. D., Michel, C. M., and Lehmann, D. 1994. Low resolution electromagnetic tomography: A new method for localizing electrical activity in the brain. *Int. J. Psychophysiol.* **18:** 49–65.

Pizzagalli, D., Lehmann, D., Koenig, T., Regard, M., and Pascual-Marqui, R. D. 2000. Face-elicited ERPs and affective attitude: Brain electric microstate and tomography. *Clin. Neurophysiol.* **111:** 521–531.

Pizzagalli, D., Pascual-Marqui, R. D., Nitschke, J. B., Oakes, T. R., Larson, C. L., Abēr crombie, H. C., Schaefer, S. M., Koger, J. V., Benca, R. M., and Davidson, R. J. 2001. Anterior cingulate activity as a predictor of degree of treatment response in major depression: Evidence from brain electrical tomography analysis. *Am. J. Psychiatry* **158:** 405–415.

Pizzagalli, D., Regard, M., and Lehmann, D. 1999. Rapid emotional face processing in the human right and left brain hemispheres: An ERP study. *NeuroReport* **10:** 2691–2698.

Posner, M. I., and Dehaene, S. 1994. Attentional networks. *Trends Neurosci.* **17:** 75–79.

Puce, A., Allison, T., Asgari, M., Gore, J. C., and McCarthy, G. 1996. Differential sensitivity of human visual cortex to faces, letter-strings, and textures: A functional magnetic resonance imaging study. *J. Neurosci.* **16:** 5205–5215.

Puce, A., Allison, T., and McCarthy, G. 1999. Electrophysiological studies of human face perception. III: Effects of top-down processing on face-specific potentials. *Cereb. Cortex* **9:** 445–458.

Puce, A., Smith, A., and Allison, T. 2000. ERPs evoked by viewing facial movements. *Cogn. Neuropsychol.* **17:** 221–239.

Regard, M., and Landis, T. 1986. Affective and cognitive decisions on faces in normals. In *Aspects of Face Processing* (H. D. Ellis, M. A. Jeeves, F. Newcombe, and A. Young, Eds.), pp. 363–369. NATO ASI Series, Nijhoff, Dordrecht.

Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., and Crommelinck, M. 2000. The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: An electrophysiological account of face-specific processes in the human brain. *NeuroReport* **11:** 69–74.

Sams, M., Hietanen, J. K., Hari, R., Ilmoniemi, R. J., and Lounasmaa, O. V. 1997. Face-specific responses from the human inferior occipito-temporal cortex. *Neuroscience* **77:** 49–55.

Sarter, M., and Bruno, J. P. 2000. Cortical cholinergic inputs mediating arousal, attentional processing and dreaming: Differential afferent regulation of the basal forebrain by telencephalic and brainstem afferents. *Neuroscience* **95:** 933–952.

Seeck, M., Lazeyras, F., Michel, C. M., Blanke, O., Gericke, C. A., Ives, J., Delavelle, J., Golay, X., Haenggeli, C. A., de Tribolet, N., and Landis, T. 1998. Non-invasive epileptic focus localization using EEG-triggered functional MRI and electromagnetic tomography. *Electroencephalogr. Clin. Neurophysiol.* **106:** 508–512.

Sergent, J., Ohta, S., and MacDonald, B. 1992. Functional neuroanatomy of face and object processing: A positron emission tomography study. *Brain* **115:** 15–36.

Streit, M., Ioannides, A. A., Liu, L., Wolwer, W., Dammers, J., Gross, J., Gaebel, W., and Muller-Gartner, H. W. 1999. Neurophysiological correlates of the recognition of facial expressions of emotion as revealed by magnetoencephalography. *Brain Res. Cogn. Brain Res.* **7:** 481–491.

Sugiura, M., Kawashima, R., Nakamura, K., Okada, K., Kato, T., Nakamura, A., Hatano, K., Itoh, K., Kojima, S., and Fukuda, H. 2000. Passive and active recognition of one's own face. *NeuroImage* **11:** 36–48.

Tabachnick, B. G., and Fidell, L. S. 1996. *Using Multivariate Statistics*, 3rd ed. Harper, New York.

Talairach, J., and Tournoux, P. 1988. *Co-Planar Stereotaxic Atlas of the Human Brain.* Thieme, Stuttgart.

Tarr, M. J., and Gauthier, I. 2000. FFA: A flexible fusiform area for subordinate-level visual processing automatized by expertise. *Nat. Neurosci.* **3:** 764–769.

Tong, F., Nakayama, K., Moscovitch, M., Weinrib, O., and Kanwisher, N. 2000. Response properties of the human fusiform face area. *Cogn. Neuropsychol.* **17:** 257–279.

Towle, V. L., Bolanos, J., Suarez, D., Tan, K., Grzeszczuk, R., Levin, D. N., Cakmur, R., Frank, S. A., and Spire, J. P. 1993. The spatial location of EEG electrodes: Locating the best-fitting sphere relative to cortical anatomy. *Electroencephalogr. Clin. Neurophysiol.* **86:** 1–6.

VanRullen, R., and Thorpe, S. J. 2001. The time course of visual processing: From early perception to decision-making. *J. Cogn. Neurosci.* **13:** 454–461.

Vuilleumier, P., and Schwartz, S. 2001. Emotional facial expressions capture attention. *Neurology* **56:** 153–158.

Watanabe, S., Kakigi, R., Koyama, S., and Kirino, E. 1999. Human face perception traced by magneto- and electro-encephalography. *Brain Res. Cogn. Brain Res.* **8:** 125–142.

Wicker, B., Michel, F., Henaff, M. A., and Decety, J. 1998. Brain regions involved in the perception of gaze: A PET study. *NeuroImage* **8:** 221–227.

Wojciulik, E., Kanwisher, N., and Driver, J. 1998. Covert visual attention modulates face-specific activity in the human fusiform gyrus: fMRI study. *J. Neurophysiol.* **79:** 1574–1578.

Worrell, G. A., Lagerlund, T. D., Sharbrough, F. W., Brinkmann, B. H., Busacker, N. E., Cicora, K. M., and O'Brien, T. J. 2000. Localization of the epileptic focus by low-resolution electromagnetic tomography in patients with a lesion demonstrated by MRI. *Brain Topogr.* **12:** 273–282.

Yamaguchi, S., Yamagata, S., and Kobayashi, S. 2000. Cerebral asymmetry of the "Top-Down" allocation of attention to global and local features. *J. Neurosci.* **20:** RC72 (1–5).